14.0 SOME CASE HISTORIES

14.1 Introduction

A substantial number of quantitative techniques have been presented in the preceding chapters. Because these methods are mainly supported by mathematical equations of various kinds, the presentation tends to suggest an exact methodology. All the user has to do is supply numbers for the equations and accurate results with appropriate confidence limits should become available. However, the real world is not like that. The techniques presented here must largely be applied in field settings and in circumstances where various uncertainties arise. Furthermore, work with the populations inhabiting large areas is always expensive and time-consuming, and various sources of bias may exist and may not be identified or corrected. Consequently, this chapter is devoted to reviewing some “case histories” to illustrate some of the problems encountered in real-world settings. Also, data from a number of the cases discussed below were used to illustrate various methods in the previous chapters, so the following sections provide some background information as to how and where the data were collected.

14.1 The Florida manatee (*Trichechus manatus latirostris*)

Manatees are slow-moving warm-water herbivores that produce a single calf at two-year intervals under good conditions, with part of the population giving birth at three-year intervals. Reproduction does not occur until age 4 or 5. Aerial surveys produced an estimate of about 1,000 manatees in Florida in the 1970's and early 1980's. Most adults carry characteristic scars from encounters with speedboats, which appear to be the principal source of mortality. A continuing increase in boating use exacerbated the situation. Concern about the accidental death rate led to initiation of a program to recover and examine carcasses in the mid-1970's. When the number recovered reached 200 individuals per year, it was widely assumed that the manatee population might soon be extirpated as the population clearly could not sustain an annual loss rate of even 10% let alone 20%. This "crisis" situation continued for another 15 years or so, with annual announcements of the imminent demise of the species. Efforts to recover carcasses were accelerated, and the aerial surveys were continued. Aerial counts are most effective during unusually cold periods, when manatees concentrate in warm water areas and are thus more readily seen. By concentrating on unusual cold-snaps and using a sizable number of aircraft, the total count was increased to approximately 2,000. However, the carcass recovery program also turned up more deaths over time, resulting in continued concern about prospects for the population. Efforts to determine survival rates and to better understand the available trend data eventually led to the conclusion that the population had, in fact, most likely actually been increasing throughout the period (Eberhardt and O'Shea 1996).

The problem was that both sources of data (aerial surveys and carcass recoveries) only accounted for some unknown fraction of the numbers present and the annual losses. At present, there is no really suitable estimate of the "efficiency" of either survey nor of the total number of manatees present in Florida waters. With the realization that the population actually was not in any real danger, it is quite possible that a relaxation of the controls on boating in manatee areas might eventually lead to a sharp reduction in the population without that event being detected by the two major surveys. Continued close attention to survival rates is thus indicated. This is not a simple matter due to the fact that scar patterns had to be used for marking. We thus have a situation where two surveys (one for population size and one for mortalities) are biased (underestimate) and there is as yet no suitable means for correcting the results. Given a suitable technique for marking, it seems likely that improved survival estimates can be obtained and will offer some protection against the very real risk that the population may decrease substantially without that fact being detected until too late.

14.2 The Pacific walrus (*Odobenus rosmarus divergens*).

The population of the Pacific walrus occupying the Bering and Chukchi seas was severely depleted by whalers starting in about 1848, and continued to be overharvested beyond the turn of the century, resulting in deaths by starvation of an appreciable part of the coastal Eskimo populations. A partial recovery was again heavily harvested for commercial purposes, starting in the 1930's. The Soviet Union prohibited taking of females by their hunters in 1957, and the population recovered to what likely was an asymptotic level by about 1980. Reproduction appeared to be substantially reduced about that time, and harvests for subsistence purposes and for ivory may well have again started an overall decline, and quite likely have reduced the male segment of the population rather sharply.

A number of efforts have been made to estimate total abundance of the walrus population through aerial surveys, but it has not been possible to demonstrate that any of these surveys have approximated the total number of walrus present due to the very bad weather often present at the times when walrus are concentrated and available for counting. The harvests are very selective, so that it is extremely difficult to determine composition of the population, and the harvest estimates depend very much on reports by hunters. Walrus ivory is valuable so there is a risk of overharvesting. Reproductive rates are roughly comparable to those for manatees, so a reduced population may take a long time to recover. Thus, while we know that there are large numbers of walrus, the prospects for ascertaining total abundance or trend are not encouraging, and the population very likely can not be adequately understood without very large expenditures of time and money.

There is evidence that walrus depend heavily on clams and that the prey species may be about as long-lived as the predator. It is thus quite possible that the extensive commercial utilization of walrus and great reductions in the population in the past may have resulted in a build-up of prey to the point where the recovering walrus population may well have "overshot" the steady-state carrying capacity of the environment in the 1980's, resulting in the observed sharp reduction in walrus reproductive rates. A very substantial fluctuation in relative biomass in the Bering-Chukchi region may well have occurred without anyone being aware of details, and the cycles might well persist over long time periods. There may be an appreciable potential for eventual human harvests of the molluscan resources of the region, leading to the necessity for the very difficult job of assessing walrus populations in detail. Thus far there are no good indices of trend, and no way to reliably estimate survival rates.

We thus have an example of a very large population [perhaps as many as 250,000, Fay et al. (1997)] that most likely has fluctuated substantially since the 1850's, with very little reliable information as to current size or trends, and few immediate prospects for improving the situation.

14.3 Bowhead whales (*Balaena mysticetus)*

At each of its meetings from 1977 to 1982, the Scientific Committee of the International Whaling Commission recommended that no bowhead whales be removed from the stock inhabiting the Bering, Chukchi, and Beaufort seas. Commercial whaling began on this stock in 1848 and continued to 1914, greatly reducing the population. From 1914 to 1970 an average of about 12 whales per year was landed by Alaskan Eskimos, so that cessation of these harvests was considered undesirable for cultural and subsistence reasons. After 1970, however, the number of whales landed increased to about 30 per year, with an increase also of whales "struck and lost", i. e., harpooned but not landed, so that as many as 100 whales may have been killed in 1977. A significant increase in the rate of removal on an already depleted population indicated a need to be concerned about possible extinction. A series of counts of northward migrating whales has been conducted in recent years, and utilized with catch data and a backcalculation model. These counts gave erratic results due to weather and ice conditions and various improvements in technique. Hence, only a single current population estimate was utilized in the model.

The bowhead calculations (Breiwick, Eberhardt and Braham 1984) provide an example of the complexities involved in attempting to assess a population trajectory with a minimum of information on reproductive and survival rates. Likely ranges of parameters had to be adopted, and many runs of the model used to explore the effects of various parameter combinations. The major concern at the time was whether or not the population would continue to recover under current and projected levels of harvest. Consequently, the analysis mainly had to evaluate the prospects for a continued decline, considering the history of harvests and current population size.

A reliable method for determining age was not available for bowhead whales. so that the available population data consisted of a classification as calves, immatures, and mature individuals. Sex ratios in the harvest and in the population appeared to be about unity so that particular complication was neglected. To utilize the information on fraction of mature animals in the population, it was necessary to use an age-structured model. Initially, it seemed realistic to combine the mature animals in a single class, thus using a reduced Leslie matrix. However, it soon became evident that high adult survival rates would bias the outcome unless lowered survival due to senescence was introduced. Hence a full matrix was used, truncated to approximate the effect of senescence. Consequently, we have the necessary but anomalous-seeming situation in which an age-structured model is used without knowledge of ages. Inasmuch a commercial harvesting had ended about 1914, and the population about 1970 was known to be at least 4,000 individuals, runs of the model with parameters in likely ranges (deduced both from the available biological data on bowheads, and on similar species) made it evident that a continuing decline was improbable under the current harvesting regime.

The important aspect of the bowhead situation for present purposes, is that the initial discussions of the problem revolved around the notion that there might only have been a few hundred whales present. The first serious efforts at a census resulted in estimates of about 1,000. Continued efforts at improving techniques ultimately pushed estimates up to nearly 8,000 whales. These efforts required about 20 years to accomplish, illustrating the fact that there is no simple way to deal with population problems in remote areas.

14.4 Grizzly bears (*Ursus arctos horribilis*)

The uncertain future of the grizzly bear in the coterminous United States resulted in a "Threatened" status under the Endangered Species Act. It is thus essential to monitor the population as closely as possible. The remaining subpopulations occupy forested habitats, are highly mobile, often secretive, and have very large home ranges. The subpopulation considered here is that of the Greater Yellowstone area, containing about 20,000 sq km, and centered on Yellowstone National Park. Direct determination of population size has thus far been very difficult, so that it has been necessary to depend on an assessment of reproductive and survival rates (obtained largely through telemetry) to assess rate of change. Reproduction occurs at about 3 year intervals, with an average litter size of about 2 cubs.

The major concern in the study is one of maintaining the isolated population in the Greater Yellowstone area. Open garbage dumps had provided a supplementary food supply since the 1920's, and likely served to concentrate the population seasonally. Closure of the dumps in the early 1970's resulted in very extensive mortalities, associated with interactions with humans in the course of seeking new food supplies. Radiotelemetry studies were initiated in 1975, and indicated a long-term decrease of about 2% per year (Knight et al, 1985), based on calculation of λ from reproductive and survival data. Estimation of survival rates has identified the key factor in maintaining the population. Adult female survival rates have been about 92%, whereas a population free of human interference should have a rate on the order of 99%. Hence protection of adult females was stressed, with a policy that a recorded loss of more than two adult females per year would be likely to jeopardize the future of the population.

Radiotelemetry data build up very slowly, so that in the initial analysis it was necessary to combine males and females in calculating subadult survival rates. As more data accumulated, it became evident that subadult male survival was appreciably lower than that of subadult females, and a revised calculation (Eberhardt et al. 1994, Eberhardt 1995) indicated that the population may in fact have been increasing. The reproductive and survival data yield an estimate of λ of 1.05, with confidence limits of about 1.00 to 1.09. Data for an index of relative abundance for Yellowstone grizzlies come from records kept of distinct family groups (females with cubs-of-the-year). Females with cubs are more readily seen than other bears, and the presence of cubs provides various clues useful in distinguishing one family group from another (number in the litter, size, coat color, radiotransmitters, etc.). Distance between sightings and various obstacles (mainly highways and the Grand Canyon of the Yellowstone River) are also important in distinguishing families. Details of the method appear in Knight et al. (1995). A major problem with using the index is simply that visibility of individual bears varies appreciably from year to year. In wet years with lush vegetation, bears are able to find adequate food supplies in relatively heavy cover and are thus not seen so readily. In dry years, they are forced to range more widely, and thus are seen more frequently.

The question of total size of the Yellowstone population has been a recurring problem. Research on Yellowstone bears in the late 1960's was concentrated on the population utilizing garbage dumps where bears were readily accessible. Marking and tagging was used to produce an estimate of population size, which was reported (Craighead et al. 1974) to be about 230 bears. Later reports (McCullough 1981) used an estimate of about 300 bears, but this number has never been documented, apparently having arisen in unpublished correspondence after the study by Craighead et al. ended. Closure of the garbage dumps in the 1970's resulted in a great deal of controversy and termination of the Craighead study. Little or no field work was done until the mid-1970's, when the population was dispersed and very much changed in behavior and general character. Estimates from tagging and recaptures or resightings were not feasible, so that, as noted above, trend had to be approximated from reproductive and survival data from the radiotelemetry work, supported in a limited way by the index of relative abundance based on tallies of females with cubs of the year.

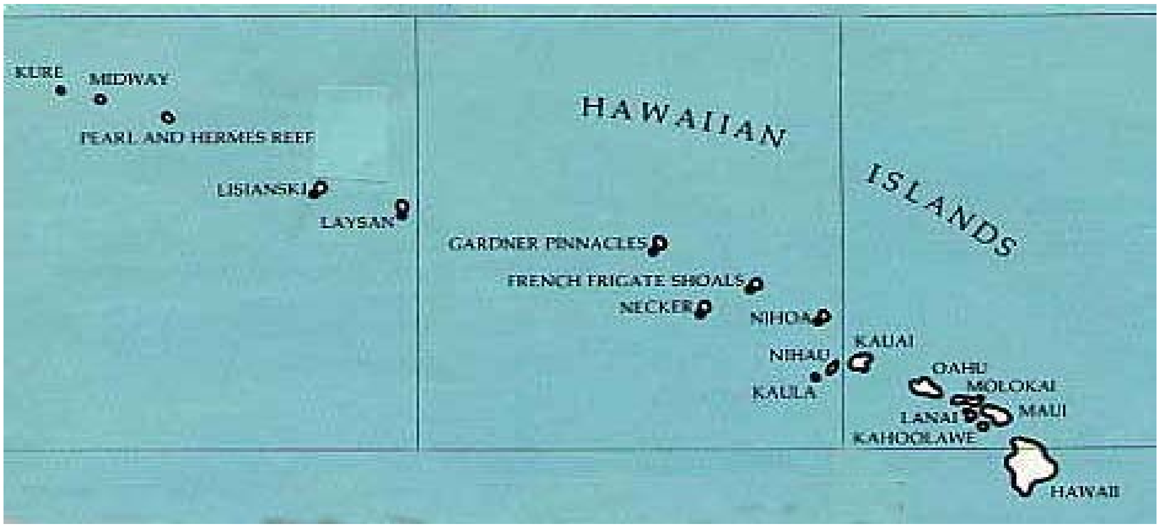
Attempts to estimate total numbers during most of the recent study depended on projections of the population size estimates from the work by the Craigheads, and the heavy losses recorded during the period of dump closures made it seem that the population must have reached a low level. Administrative and public requests for an estimate ("How many are there?") led to construction of minimum estimates in the recent study, starting with the tally of adult females with cubs. Although these estimates were described as minimums, many public reports treated them as estimates of actual numbers. Ultimately it became possible to utilize the accumulated data on sightings to produce a direct estimate of recent numbers (Eberhardt and Knight 1996). This data suggested that the current population may be on the order of 400 bears. Although the variable nature of the available data resulted in wide confidence limits, it does seem likely that the estimates of the late 1960's were biased downwards by the use of data collected mainly at the garbage dumps, and that the population was then larger than supposed. Mortalities associated with closure of the dumps thus very likely did not result in as abrupt a decrease in numbers as seemed apparent at the time, and the recovery may have been much more rapid than generally assumed. Focussing on total numbers thus seems to have greatly confused the issues.

The intense controversy over dump closure resulted in the abrupt termination of the Craighead study with little or no monitoring of marked bears. The subsequent study did not begin marking until 1975, and then initially only outside of Yellowstone National Park. It thus took nearly 10 years to build up sufficient information to approximate a population analysis (Knight and Eberhardt 1985). Had the early study been continued throughout the period of dump closure, the long interval of uncertainty about status of the population might have been reduced appreciably. However, the Craighead study depended largely on visual resightings of marked bears at the dumps, while the recent study has utilized radiotelemetry of bears trapped at various places throughout the Park. Whether continuation of the field studies during the dump closure would have reduced the confusion is thus not certain. It does seem evident that the emphasis on population size led to continued confusion and uncertainty. To estimate the actual numbers of bears in the Greater Yellowstone area by a capture-recapture technique would be extremely expensive and might not succeed. Live-trapping would be required which presumably calls for moving traps by helicopter (not permitted in Wilderness Areas, which are an important component of the overall bear habitat). Because female survival is crucial, it may well be that this is the essential parameter to monitor.

14.5 Hawaiian monk seals (*Monarchus schaundslandi*)

The Hawaiian monk seal is known to be sensitive to human intrusions, and has been sufficiently reduced in numbers to become classified as "Endangered" under the Endangered Species Act. An as yet poorly understood series of events resulted in redistribution of the population over the several atolls of the Northwestern Hawaiian Islands which constitute the sole habitat of the species). Abundance was sharply reduced in the western part of the chain, leaving a severely imbalanced sex ratio, with adult males substantially outnumbering females in at least two sites. The excess of males has resulted in a breeding phenomenon known as "mobbing" behavior in which females may be killed outright or injured sufficiently to lead to death from shark predation. Population trends are available as "beach counts" and survival and reproductive data are available from data on marked seals.

Six primary sites contain the majority of the population. Midway Atoll was subjected to intense military activity in World War II, and was used extensively by the U. S. Navy until recent years. This intense human activity essentially extirpated the monk seal population, with mean beach counts of about 50 seals observed in 1956 and 1957. Apparently these were very old seals, and they were mostly gone by the late 1960's. A few seals moved in from the adjacent sites (Kure Atoll and Pearl and Hermes Reef), so that mean beach counts on the order of 10 seals were observed recently. All of the other major sites, with the exception of the easternmost, French Frigate Shoals, exhibited a sharp decline beginning in the 1960's. It is likely that there was a common agent external to the individual populations that caused the decline, but a specific cause has not been identified. Occupation of Kure for operation of a Loran station is known to have contributed to the decline there, and efforts were made to rebuild the population by introducing young seals rescued from French Frigate Shoals and "rehabilitated" in captivity for a year. A disease of unknown origin turned up in seals kept in captivity for use in the rehabilitation effort, resulting in cessation of that activity.



Locations of the monk seal sites in the Northwestern Hawaiian Islands

No human actions are known to have impinged on the population at Pearl and Hermes Reef, but it was driven to a very low level in the 1960's going from beach counts of more than 200 seals to a low of about 40 around 1975, followed by a steady increase in numbers. Adult sex ratios of as high as 3 adult males to each adult female were observed on Laysan and Lisianski in the 1970's, and the population on Laysan continued to decline slowly, possibly associated with the "mobbing" phenomenon. Numbers on Lisianski are essentially static. Mating occurs in the water, and the excess males simply gang up on estrus females, doing severe damage in the process. I believe that the agent responsible for the overall decline was somehow selective by sex, resulting in the unbalanced sex ratio. Apparently the decline was so severe at Pearl and Hermes that it affected adult males as well. Initial counts at Kure showed an excess of males, but the introduction of subadult females has brought the overall sex ratio into balance.

The situation at French Frigate Shoals was quite different. A Loran station was located on the best pupping site (East Island), and removal of that station was followed by a steady increase in the population, continuing up to the late 1980's, when a major decrease began, more than halving the population there. This decrease has been marked by starvation of weaned pups, and seems quite clearly a consequence of reduction in an essential food source. As yet there has not been a shift in adult sex ratios, and it seems likely that the situation is entirely different from that at the western sites in the early 1960's.

An intensive program of tagging weaned pups was started in the early 1980's, and has resulted in the presence of a substantial marked cohort in the population. Intensive studies at Laysan Island have also yielded a good deal of reproductive data. Because the reproductive data at the other sites are not as extensive, it has been necessary to use the Laysan values to explore trends at the other sites. These results can, however, be supplemented by rates of change estimated from the recent beach count data (by log-linear regression).

A report on status of the population (Gilmartin and Eberhardt 1995) illustrates the sharp decline in the early years (1960's). Currently, the smaller, western populations (Kure, Midway, Pearl and Hermes Reef) appear to be increasing, while the two intermediate populations (Laysan and Lisianski) are static or decreasing slowly. The French Frigate Shoals population increased while the other populations were decreasing in the 1960's (tagging shows only minor movements between individual populations), peaked in 1988 or 1989, and then dropped dramatically in consequence of persistent starvation of weaned pups.

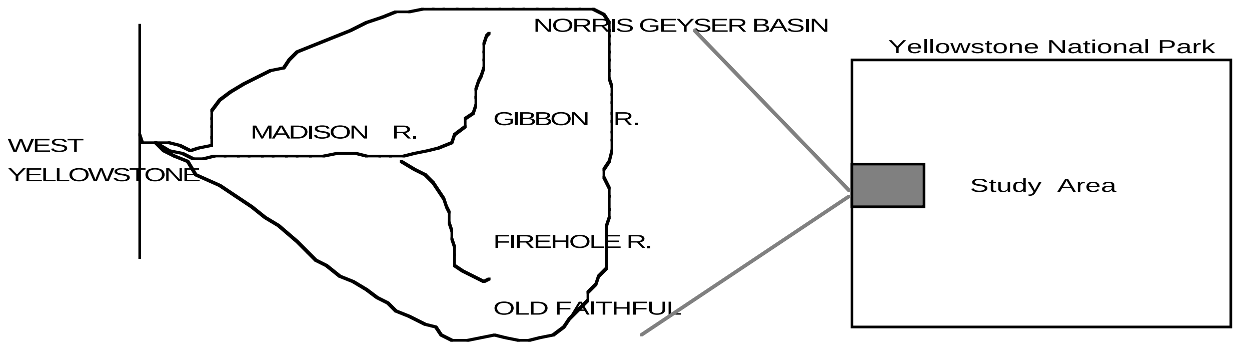
The monk seal data are particularly interesting because there is no clear evidence of causes of the initial major decline. Because adult sex ratios were dramatically shifted (about 3 adult males per adult female) and subsequent data show the usual large mammal pattern of lower male survival, one can only conclude that the decline resulted from some human activity, but this conclusion is unsupported by data (and largely not discussed in the literature or in reports on monk seals). The essentially static population on Lisianski and Laysan is characterized by reduced adult female survival, but again no cause has been identified. The "crash" at French Frigate Shoals is clearly due to resource limitation, but again the cause is unknown. Quite recently monk seals have begun to move into the main Hawaiian Islands. They have not previously been known to occupy these islands, but may simply have been extirpated by the earliest Polynesian inhabitants, without any archeological or other record becoming available as yet.

14.6 The Madison-Firehole elk herd

The study and data described below are included to provide an example of circumstances where a natural population has remained remarkably constant in the face of severe and variable winter conditions.

The study system

The Madison-Gibbon-Firehole drainage (general location sketched below) consists of a rugged mountainous landscape with elevations ranging from 2150-2800 meters. The pronounced topography results in variable aspects and slopes supporting a diversity of plant communities, including mature conifer forests, sedge-grass meadows, and aquatic communities. Numerous geyser basins warm low-elevation meadows and rivers, thereby reducing snow cover in these areas and enabling some unique plant associations to continue photosynthesis throughout the winter. Large scale fires during 1988 burned 55% of the drainage, creating a complex mosaic of burned and unburned forests at different stages of succession. Winter climatic factors are an important abiotic component of the ecosystem, as snow depths frequently exceed 1.2 m, drastically reducing food availability and producing severe energetic bottlenecks for herbivores during the winter.



Sketch map of the study area, which includes the Madison, Gibbon, and Firehole River drainages.

The approximately 500-600 elk residing in the area are nonmigratory, remaining within the borders of the Park throughout the In the 10 years of study to date, no radio-marked elk has left the study area, nor have any of these elk moved outside the 3 river drainages constituting the study area (based on approximately 7,000 radio-locations). Neither the landscape nor the elk that inhabit this drainage have been manipulated to any significant extent since European settlement, hence the elk population is regulated solely by natural processes. This is a particularly unusual feature of this study system since nearly all large herbivore populations in North America are harvested by man, including the previously studied Northern Range elk population of Yellowstone National Park (Houston 1982). Human harvest regimes dramatically influence nearly all demographic attributes and processes within a population. The only anthropogenic influence that may have appreciably impacted the natural dynamics of the Madison-Firehole elk population is the extirpation of wolves from the Park in the early part of this century. Reintroduction of wolves was initiated in 1995, with the first releases of wolves into the Madison-Firehole drainages occurring in spring 1996. Elk and bison are the only ungulates with substantial numbers in the area. A few mule deer and an occasional moose may be seen, but do not constitute a significant prey base.

Population data

In the fall of 1991, 5 years prior to initiation of wolf reintroductions in Yellowstone National Park, intensive telemetry-based investigations of the landscape-use patterns and demographic characteristics of the elk population were initiated. The sedentary nature of these animals, combined with the protection afforded by the Park and frequent contact with humans, has resulted in animals throughout this drainage becoming relatively tolerant of humans. This tolerance greatly facilitates opportunities to economically capture and mark animals using ground-based delivery of immobilizing drugs via dart rifle. Once marked, animals can be frequently monitored with hand-held telemetry systems and observed for quantification of survival, cause of death, habitat use and distribution patterns, feeding behavior, and the collection of snow-urine and fecal samples for indexing nutritional and reproductive status. These ongoing studies represent the most current and extensive databases on elk in Yellowstone National Park.

A sample of 30-40 females, ranging from 1 to 15 years of age and instrumented with radio collars has been maintained throughout the study.

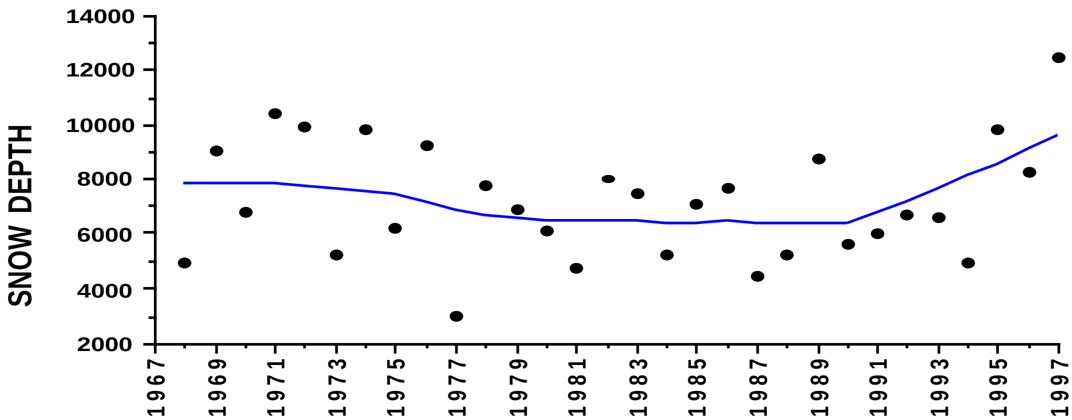
Intensive field studies, involving one or more graduate students and 1-2 technicians have been conducted annually from December thru April, with low-level monitoring of all animals occurring through the rest of the year. Data on survival beyond age 1 has been accumulated along with reproductive performance. Very high pregnancy rates have been observed, along with high survival beyond age 1 for the first 5 years of the study. Transmitter performance has been nearly perfect, and no mortalities were observed in the first 3 years of the study. These data provide an annual survival estimate for prime-age females (1-11 years of age) of 97%. Survival rates for prime age classes in the study were much the same as those reported by Houston (1982) for the northern Yellowstone elk herd, but dropped off sharply after age 11, while Houston's data suggest high survival continuing out to age 16 or beyond. Preliminary findings from the Madison-Firehole study indicate that high fluoride and silicate concentrations in area vegetation may induce accelerated tooth wear and thus early senescence.

Pregnancy rates of all instrumented elk were also assessed each year using serum and fecal steroid assays providing a pregnancy rate estimate of 92% for animals >2 years of age. As expected, yearling pregnancy was lower, estimated at 40%. Both survival and pregnancy rates were reduced during the 6th year of the study (1996-97), which was the severest winter recorded in the past 60 years. Reproductive rates observed in the Madison-Firehole area also closely approximated those for the northern herd.

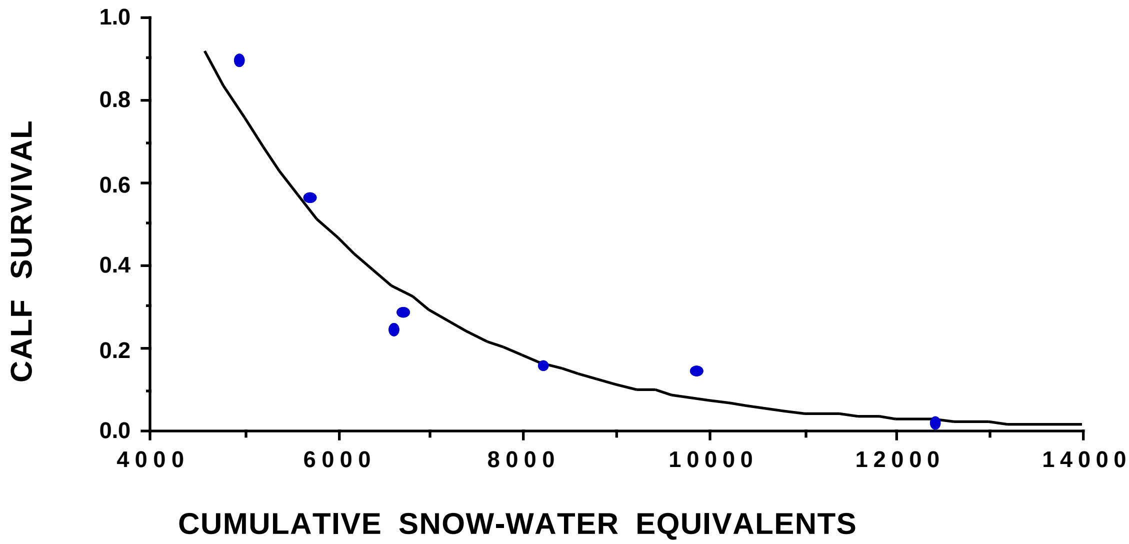
Population size was estimated from aerial surveys conducted during the first 4 years of the study. These surveys utilized the radiocollared elk and Petersen estimates. In April of 1997, estimates using ground counts were begun. These counts were conducted just after the meadows became snow-free, and elk ere concentrated at these sites. Petersen estimates were obtained from 10 such ground surveys conducted in the spring of each year, and used to estimate population size after winter mortality had ended. Because survival over the summer and early fall is virtually 100%, similar counts in October were used to estimate recruitment of calves born in the summer, and thus approximate a total population size.

The estimates of recruitment and early survival depend on large samples (1,000 to 1,500 observations each year) of calf-cow ratios, taken during the months of December through April. In all years calf-cow ratios decreased from about 42-48 calves per 100 cows in December to April ratios ranging from 38 to <1 calves per 100 cows. The April ratios are closely related to cumulative snow depth data, with the highest observed ratio associated with the year (1993-94) of lowest snow depth. Because adult cow survivals were very high, the drop in calf-cow ratios is evidently mainly a function of over-winter calf mortality.

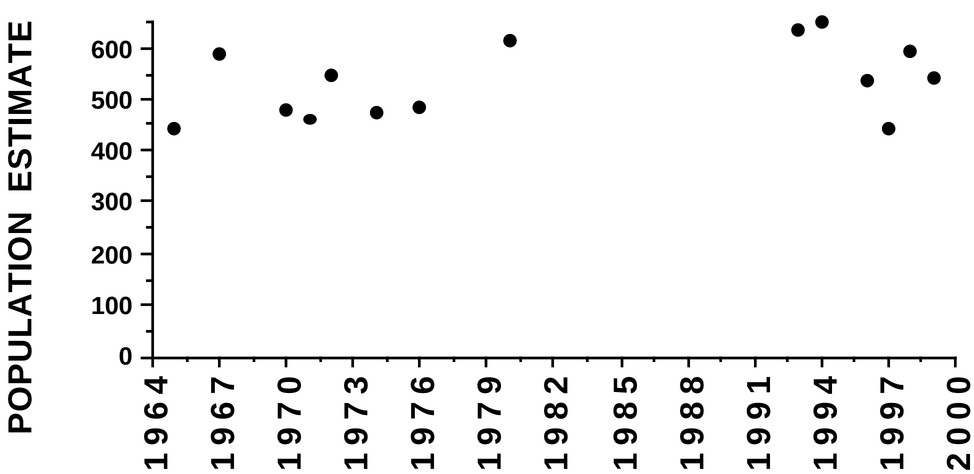
Snow depth records (an automated weighing system is used) are available for the last 30 years (see graph below). These records can be used to demonstrate that the calf-cow ratio decreases markedly with increasing spring snow depths. The mild winter of 1994 was associated with a high spring calf-cow ratio (38), while the severe winter of 1996-97 resulted in the lowest such ratio reported (<1 calf per cow in the spring).



Snow depths recorded over the last 30 years in the Madison-Firehole study area.



Calf survival and spring snow depths, measured as snow-water equivalents. An exponential curve was fitted to the data.



Population trend of Madison-Firehole elk population.

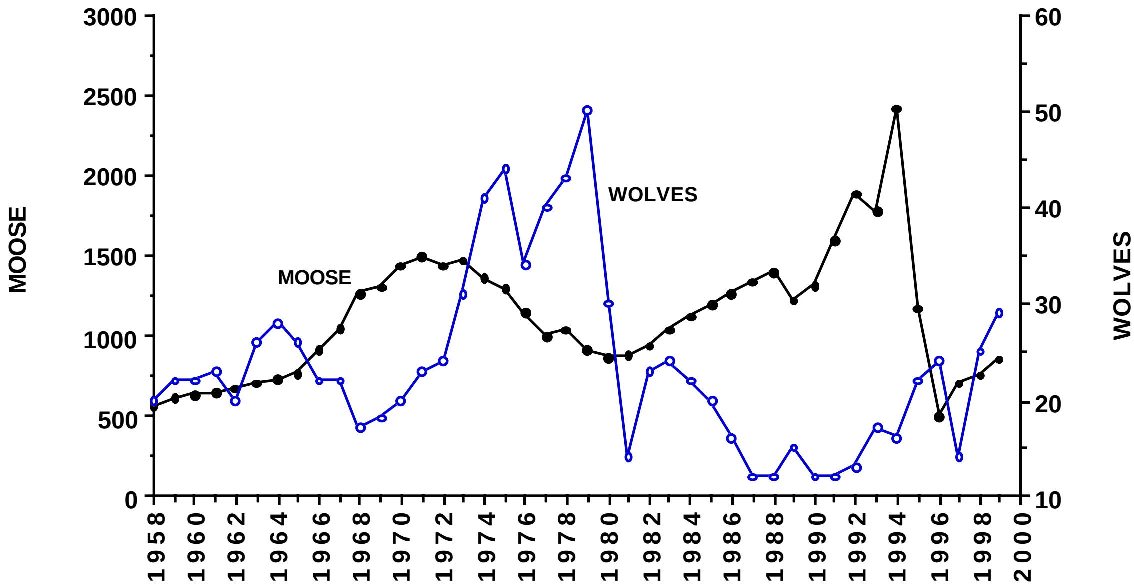
In spite of the dramatic effect of over-winter snow depths on calf survival, the population has remained remarkable constant due, we suspect, to a density-dependent mechanism which most likely results from a strict limitation on numbers of individuals that can be accomodated in the thermal refugia. This impact appears to fall principally on calves, inasmuch as adult cow survival has remained high. Wolves have begun to take significant numbers of calves, and some adult elk, so it will be particularly interesting to see how they influence this relatively stable population.

14.7 Isle Royale wolves and moose.

An appraisal of the Isle Royale moose and wolf data using eqs. (12.34) and (12.35) suggests the possible utility of these equations for further wolf-ungulate studies (Eberhardt 1998, Eberhardt and Peterson 1999). Further examination of the data suggests that eq. (12.35) seems to be roughly satisfactory as a model for the moose data, at least up to the point where a tick epizootic influenced the population for several years (starting in 1989), but the ratio-dependent model for wolves does not give a very good fit to the trend of the Isle Royale wolf population. Hence, the issues of how to test such a fit need to be further examined with the data. The concept of ratio-dependence has been criticized in the literature (as well as defended), and thus needs further attention. It is also quite possible that the Isle Royale wolves may be influenced by the limitations of an island (544 km. sq.) habitat, and be responding to that limitation to the point where it limits utility of the ratio-dependent model.

Several papers (Messier and Crete 1985; Messier 1994, Gasaway et al.1992) have proposed models for wolf-ungulate interactions having two equilibrium states, one (the upper) induced by resources available to the ungulates, and the second (lower) presumably induced by predation. The data thus far analyzed do not support these models (Eberhardt 2000), and need to be further assessed, along with the prospects for a "predator-pit" type of lower equilibrium. The analysis will necessarily be somewhat speculative for lack of data on multiple-prey situations, but it does seem that there is enough data to raise questions about the possible existence of such an equilibrium in wolf-ungulate interactions.

For purposes of the present assessment, however, it may be instructive to compare the trends of Isle Royale moose and wolf populations (shown below) with the theoretical model of Fig. 12.5. That model predicts an equilibrium would be reached after about 20 years, starting with a large moose population and a few wolves. On Isle Royale there has been little indication of an equilibrium state as yet. However, parvovirus was reported in the wolf population in about 1980 (Dr. R. Peterson, personal communication) and apparently drove it to low levels which have persisted until quite recently. The moose population then increased steadily and ultimately crashed in a very severe winter. If the “predator pit” models are correct, one might expect the moose population to continue to be suppressed by wolves. It will be interesting, and hopefully instructive, to see how the trend of Isle Royale moose and wolf populations compare with those of Yellowstone elk and wolves.



Trend of moose and wolf populations on Isle Royale.